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Nutrient limitations in an extant and drained poor fen: implications for restoration

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Abstract

In a species-rich poor fen (*Caricetum nigrae)* and a species-poor drained fen, the difference in nutrient limitation of the vegetation was assessed in a full-factorial fertilization experiment with N, P and K. The results were compared to the nutrient ratios of plant material and to chemical analysis of the topsoil. A rewetting experiment with intact sods was carried out in the glasshouse and the results are discussed in view of restoration prospects of drained and degraded peatlands. In the undrained poor fen the above-ground biomass yield was N-limited while the vegetation of the drained fen was K-limited. Experimental rewetting of intact turf samples, taken in the drained site, did not change the biomass yield or the type of nutrient limitation. It was concluded that mire systems which have been subjected to prolonged drainage are inclined to pronounced K-deficiency, probably due to washing out of potassium and harvesting the standing crop. This may hamper restoration projects in degraded peat areas where nature conservation tries to restore species-rich vegetation types with a high nature value.

Introduction

In industrialized countries nature conservation is currently engaged in attempts to restore endangered vegetation types (Gough & Marrs 1990; Van Diggelen et al. 1991; Berendse et al. 1992; Poschlod & Jordan 1992; Wheeler et al. 1995; Galatowitch & Van der Valk 1995; Pfadenhauer & Klötzli 1996). Many of these endangered vegetation types are found in mires and wet grasslands on peaty soils, which are surrounded by agricultural areas with low water tables. Despite sometimes legal protection they are still influenced by drainage and fertilization (Bakker & Olff 1995; Grootjans & Van Diggelen 1995; Pegtel et al. 1996).

The impact of drainage on organic soils is rather complex. It is known that severe drainage causes both physical and chemical changes of the peat soil. The structure of the peat changes and the water holding capacity is affected negatively (Kayak & Okruszko 1990). Rapid mineralization of organic material causes a dramatic release of nutrients in most fen peats (Okruszko 1977; Janiesch 1978; Grootjans et al. 1985). Nitrate in particular becomes available for the vegetation in large quantities (Grootjans et al 1986; De Mars et al. 1994). When present in large amounts, calcium and aluminium may reduce P-availability and under aerobic conditions (high redox potential) iron can chemically fix phosphate and render it unavailable for plant growth (Richardson & Marshall 1986; Sah & Mikkelsen 1986).

The question is whether it is possible to reverse the negative effects of drainage. Nature restoration activities are often aimed at lowering the soil fertility. But when dealing with wet vegetation types in particular, the effects of such practises are often nullified when the hydrological site conditions are not restored (Bakker 1989; Klötzli 1987; Grootjans & Van Diggelen 1995; Okruszko 1995).

Rewetting stimulates the creation of anaerobic environments, and selects against species which are not adapted to these circumstances. Rewetting also has a major effect on the availability of macro-nutrients because it reduces mineralization and stimulates denitrification which lowers nitrogen availability (Patrick & Tusneem 1972; Prentki et al. 1978; DeLaune et al. 1981; Grootjans et al. 1985). Hauschild & Scheffer (1995), however, found that rewetting of relatively acidic fen peat soils may even increase nitrification. In a laboratory experiment with degraded fen peat soils the highest nitrate accumulation was found in samples which were completely rewetted (100% WKmax). The high content of easily decomposable organic substances in degraded but relatively acid peats was thought to be responsible for the increase in nitrification. Under field conditions increased NH_4^+ concentrations in the topsoil have been observed after rewetting (Eschner & Liste 1995). Furthermore, anaerobic conditions may increase the phosphate availability, due to low redox potentials which cause the dissolution of iron phosphates (Patrick & Khalid 1974; Caraco et al. 1989; Roelofs 1991). Therefore rewetting potentially leads to increased availability of nutrients for marsh plants adapted to anaerobic conditions.

The role of potassium in rewetting is, however, poorly understood. Kayak & Okruszko (1990) found that in an intensively managed grassland the total amount of potassium in a fen peat soil was hardly sufficient to ensure crop production. De Mars et al. (1996) suggested that drainage of peat soils causes a sharp decrease in potassium availability due to leaching. Once leached, potassium will not be easily available after rewetting, since the concentration of potassium in ground- and rainwater is usually very low.

In our research, we consider the soil deficient in one ore more nutrients when the above-ground biomass increases after supply of these nutrients. We will focus on the following questions: (1) do well-developed poor fens and severely drained ones differ in the type of nutrient limitation; (2) which species determine the nutrient limitation for a vegetation and (3) does the type of nutrient limitation change after rewetting a drained peat soil? To answer these questions we applied three approaches: (a) chemical analyses of the top soil; (b) fertilization in the field and in the glasshouse; (c) rewetting of turf in a glasshouse.

Methods

Site description

The study area is located in the middle course of the ‘Zwarte Beek nature reserve’ near Hasselt in Belgium (56 °61′ N, 6 °60′ E). Its upper course is situated on the ‘Kempens plateau’ and is almost completely surrounded by heathland and forests. Consequently, the narrow river valleys in this region are hydrologically intact and not influenced by intensive agricultural activities. The middle course, which is wider and managed by nature conservation, is severely influenced by a deep drainage ditch situated in the centre of the reserve parallel to the meandering Zwarte Beek. This ditch, called ’Oude Beek’ (Old Stream) drains the peatlands on either side (Aggenbach et al. 1990). The drained site was established close to this drainage ditch. The vegetation consisted mainly of *Agrostis canina* and *Juncus effusus*. The undrained poor fen, further called ‘the wet site’, was situated further away from the drainage ditch in a former turf pond, which receives much ground water from the surrounding infiltration areas (Aggenbach et al. 1990). The vegetation in the wet site was dominated by *Carex rostrata*, *Carex nigra*, *Lotus corniculatus*, *Equisetum fluviatile*, *Potentilla palustris* and *Filipendula ulmaria*. *Calliergonella cordifolium* and *Brachythecium rutabulum* dominate the moss layer.

Soil sampling and analyses

In August 1993, three soil samples were taken randomly with a soil corer to a depth of 10 cm. This procedure was repeated three times for each site resulting in three mixed soil samples per site. The samples were analyzed for pH(H_2O) after addition of 20 ml of demineralized water to 15 g fresh soil and pH(KCl) after adding additionally 2.5 ml 1M KCl. The remaining part of the soil samples were air dried (40 °C), ground and analyzed for organic matter (by loss-on-ignition at 950 °C for 3 h), Pw-index (extraction in water 1:60 v/v (Sissingh 1969)), total nitrogen (by a modified Kjeldahl technique (Wieninger 1936), total phosphate (Murphy & Riley 1962), total potassium (AAS measurement after extraction with 5% HCl), moisture content (15h at 105 °C), CEC (Ca measurement using AAS after percolation with calcium acetate at pH 8.2 and at pH 6.5 followed by percolation with water and with 1M NaCl). Base exchange was determined using AAS measurement after percolation with 1M NH_4NO_3 for exchangeable K and Na, and flame emission spectrophotometric measurement after percolation with 1M NaCl for exchangeable Ca and mg. H^+-titration was done with 0.1 m NaOH and with phenolphthalein.

Water sampling

Two piezometers (1.66 m and 3.86 m deep) with filters of 30 cm were installed close to the fertilization experiment in the wet site. Ground water samples were collected fortnightly using a syringe and tube in the growing seasons of 1993 and 1994. Soil water samples were collected from three small perforated plastic tubes that were inserted in the upper horizon. pH, EC and redox were determined in the field. All samples were filtered on site with a Millipore 0.45 μm filter. One portion of the filtered sample was acidified with a drop of HNO_3 conc. in a 10 ml tube. This was used for the determination of metal cations on a plasma-emission spectrophotometer. Another portion was not acidified and used for determination of anions and NH_4^+ on a Skalar auto-analyzer.

Fertilization experiment

The fertilization experiments in the field was carried out according to a full-factorial design. In 1992 Boeye et al. (1997) started a fertilization experiment with N and P in the wet site. We continued the N and P fertilization in the first week of April 1994, and established extra plots for K fertilization. Eventually, the experiment consisted of 8 fertilizer treatments, each replicated 5 times: none, N, P, K, NP, NK, PK and NPK. In the drained site, 40 new plots were established, measuring 0.60×0.60 m separated by a distance of 0.4 m. In both sites the vegetation was cut before fertilization to have similar initial conditions in all plots. Slow release fertilizers (trade 'Osmocote') were applied in amounts of 200 kg/ha N as $CO(NH_2)_2$, 80 kg ha^{-1} P as $Ca(H_2PO_4)_2H_2O$ and 200 kg ha^{-1} K as K_2SO_4. All plots were harvested the second week of August 1994. The harvest of the square of 0.6×0.6 m^2 was taken to be dried (24 h. at 70 °C) and weighted. The above ground biomass of individual species was assessed in a sub-plot of 0.2×0.2 m^2.

Chemical analyses of plant material

All vegetation samples harvested in the fertilization experiment were analyzed for N, P and K. The dried samples (24 h. at 70 °C) were ground in a centrifugal mill. Nitrogen-content was determined by a modified Kjeldahl-method (Wieninger 1936). After destruction with a mixture of sulphuric acid and perchloric acid the P-content of plant tissue was measured using spectrophotometry with molybdate blue. The K-content was measured using AAS.

Double pot experiment

Undisturbed circular turf samples (⌀ 20 cm) to a depth of 10 cm were collected in the third week of April 1994. Twenty turf samples from the wet site and forty from the drained site were taken and transported in plastic rings to an open glasshouse. A perforated bottom (every cm a hole with a diameter of 2 mm) was fitted underneath the turf from the wet site, which were then placed in a (12 l) bucket with demineralized water and later a nutrient solution. The turf was only 10 cm thick because this zone contains the major part of the plant roots and because otherwise many roots would not grow deep enough into the soil to penetrate the perforated plate and reach the nutrient solution. The section of turf samples taken from the drained field was split into two groups. The first half was placed on a perforated plate on top of a bucket to imitate drained conditions. The other half was rewetted and treated similar to the turf taken in the wet site. A schematic representation is shown in Figure 1. The pots were placed randomly on a table in the glasshouse.

The turf samples were initially placed on demineralized water. After two weeks, when roots had grown into the buckets, the water was replaced by various nutrient solutions. Turf on demi-water served as a control. The experiment, therefore, consisted of three series of five different nutrient treatments with four replicates which resulted in a total of 60 pots. The complete nutrient solution was composed (in mmol l^{-1}) of 8.0 NO_3^-, 0.7 $H_2PO_4^-$, 4.7 K^+, 1.3 Mg_2^+, 2.3 SO_4^{2-} and 1.5 Ca^{2+} (The ground water in the 'Zwarte Beek' study area is very Ca-poor; Aggenbach et al 1990). KCl was used as a substitute for KNO_3^- when nitrogen was omitted, and also to replace KH_2PO_4 in the P-deficient solution. In the solution in which potassium was omitted, sodium was used as a substitute. Trace elements were provided in the following concentrations (in μmol l^{-1}): 35 Fe (as Fe-DTPA), 10 Mn (as $MnSO_4.H_2O$), 20 B (as $Na_2B_4O_7.10H_2O$), 3 Zn (as $ZnSO_4.5H_2O$), 0.5 Mo (as $(NH_4)_6Mo_7O_{24}$) and 0.5 Cu (as $CuSO_4.5H_2O$).

The samples were clipped four times, every sixth week in order to enhance the nutrient impoverishment of the soil. The total duration of the experiment was 26 weeks. Fresh nutrient solutions were provided every three weeks. The total yield of the vegetation under a particular nutrient treatment consisted of the cumulat-

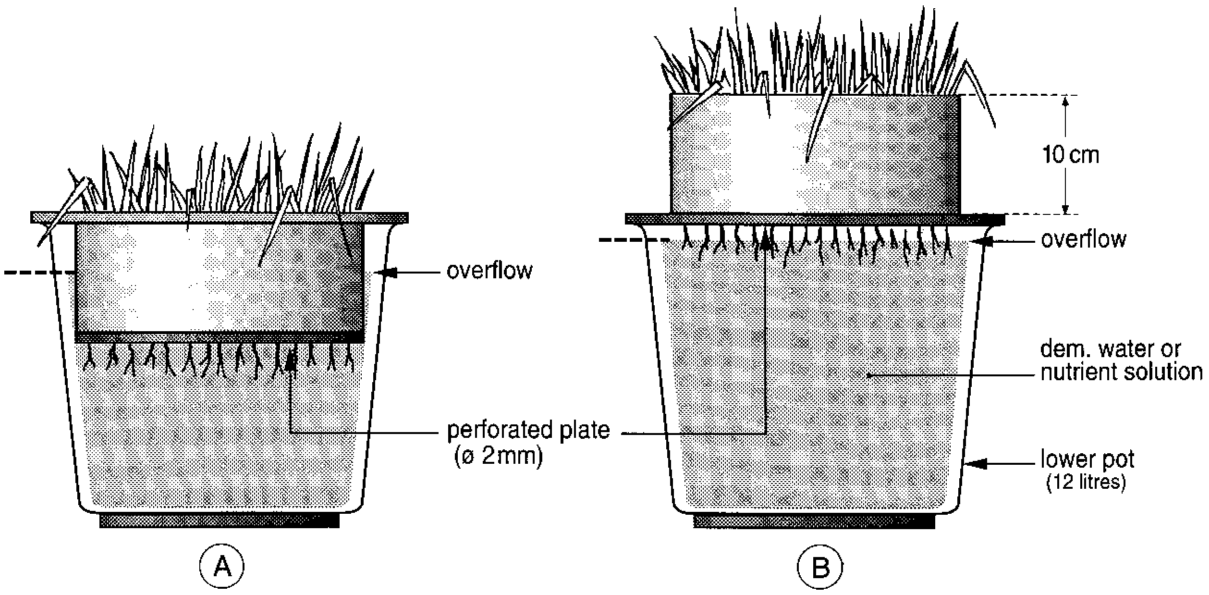

Figure 1. Experimental setup for the assessment of nutrient limitation with intact turf samples. In the drained treatment, the samples were placed on top of a bucket (right) while in the wet and rewetted treatment the turf samples were placed in a bucket (left). The vegetation could obtain nutrients both from the soil and from a nutrient solution. The nutrient solutions used were: complete (containing all nutrients), N-deficient, P-deficient, K-deficient, and as a control H_2O.

ive dry above-ground biomass of all harvests per pot. The reduction of total yield per treatment compared to the total biomass yield under complete nutrient supply was taken as a measure for nutrient limitation.

Statistical analyses

Differences between the soil analyses of the wet and drained sites were tested using a Mann–Whitney U-test. Since there was no overlap between the sites in any of the variables the low number of replicates gave no problem. The effects of the nutrients (N, P, K) and the difference between the sites (wet, drained) and the statistical interaction between the sites and nutrients was tested with an ANOVA with four factors, suppressing the effects of interactions between nutrients. A *t*-test was used to test the significance of differences between the treatments and the control. Since the effect of the fertilizer combinations (NP, NK, PK and NPK) on the standing crop are not identical to statistical interactions, this was tested as well using a three-way ANOVA. The same procedure was used to test the effects of nutrients on the biomass of individual species (only when $n > 10$). The parameter estimates for the main effects and the interactions were calculated according to Olff (1992) to find out whether the effects or interactions were positive or negative.

Results

Soil chemical analyses

All chemical parameters in the topsoil were higher in the wet than in the drained site (Table 1). The pH was clearly higher in the wet site and the organic matter content was almost three times as high ($p < 0.05$). The total K content was almost six times higher in the wet site compared to the drained site ($p < 0.05$).

Ground and soil water sampling

Close to the wet site, where the water samples were taken (Table 2), ground water discharge is obvious (Boeye pers. comm.). The ground water discharge, therefore, provides the topsoil with N (as NH_4^+, NO_3^- was absent), P, Fe and Ca. NH_4^+ PO_4^{3-} were lower in the soil water, probably due to plant and microbial uptake and other losses (denitrification and P-fixation). Iron was much higher and apparently concentrates in the upper soil horizon. Calcium behaved more or less

Table 1. Soil characteristics of a wet, well-developed *Caricion curto-nigrae* and a drained, degraded site in the Zwarte Beek nature reserve. Significance of differences ($p < 0.05$) was tested using a Mann–Whitney U-test ($n = 3$).

Variable	Wet site	Drained site	Significance
pH-H_2O	5.07±0.03	4.37±.07	*
pH-KCl	4.37±0.03	3.80±.06	*
Org. matter (g/100 g)	70.83±2.07	24.77±4.82	*
Pw-index (mg P_2O_5/L)	30.0±4.5	6.3±1.7	*
N-tot (g N/100 g)	1.45±0.05	0.66±0.02	*
P-tot (mg P_2O_5/100 g)	1094±95	657±32	*
K-tot (g K_2O/100 g)	0.240±0.006	0.043±0.001	*
Moisture content (g H_2O/100 g)	602±16	128±5	*
CEC (me/100 g)	67.4±1.0	30.9 ± 0.7	*

Table 2. Ground water analyses in a species-rich wet fen vegetation (*Caricion curto-nigrae*)

	pH	EC_{25} (μS cm^{-1})	redox (mV)	NH_4^+ (mg l^{-1})	PO_4^{3-} (mg l^{-1})	Fe (mg l^{-1})	Ca
Deep piezometer	6.6±0.24	148±4.4	102±17.6	0.27±0.05	0.69±0.30	5.7±2.54	18±0.6
Shallow piezometer	6.6±0.24	147±3.1	107±18.9	0.23±0.07	0.85±0.15	5.5±2.20	18±0.6
Soil water	6.4±0.24	328±83	86±24.4	0.12±0.18	0.12±0.41	65±39.0	20±4.3

conservative. Unfortunately, no reliable readings of K could be made because of technical problems.

Factorial fertilization

Peak standing crop after the different fertilization treatments in both sites is shown in Figure 2. Compared to the control, only N addition in the wet site and NPK addition in the drained site increased the above-ground biomass yield significantly (both $0.01 < p < 0.05$). The overall three-way ANOVA showed a significant effect of the factor site on the standing crop ($p < 0.001$). There were significant effects of both N and K ($0.01 < p < 0.05$) but no significant interactions were observed of the single nutrients with the factor site. The three-way ANOVA per site showed a significant stimulating effect of N on the biomass yield in the wet site ($0.01 < p < 0.05$) and of K in the drained site ($0.001 < p < 0.01$).

Plant species responses

In the field fertilization experiment in the wet site, several effects of different nutrients were observed for individual plant species. The effect of N on the total standing crop was mainly due to the increased biomass of *Filipendula ulmaria* ($0.01 < p < 0.05$). No other plant species showed a significant effect of N except a negative interaction between N and P for *Juncus sp.* ($0.01 < p < 0.05$) and also a negative interaction between N and K for *Epilobium palustre* ($0.01 < p < 0.05$). Phosphate addition resulted in an increase in biomass of *Sparganium erectum* ($0.01 < p < 0.05$) and a decrease of *Potentilla palustris* ($0.01 < p < 0.05$). The latter increased its biomass after K addition ($p < 0.001$) while *Equisetum fluviatile* showed a decrease in biomass ($0.01 < p < 0.05$).

Grasses dominated in the drained site and were responsible for the increase in biomass after K addition ($0.01 < p < 0.05$). Furthermore an interaction between N and K was assessed ($0.01 < p < 0.05$).

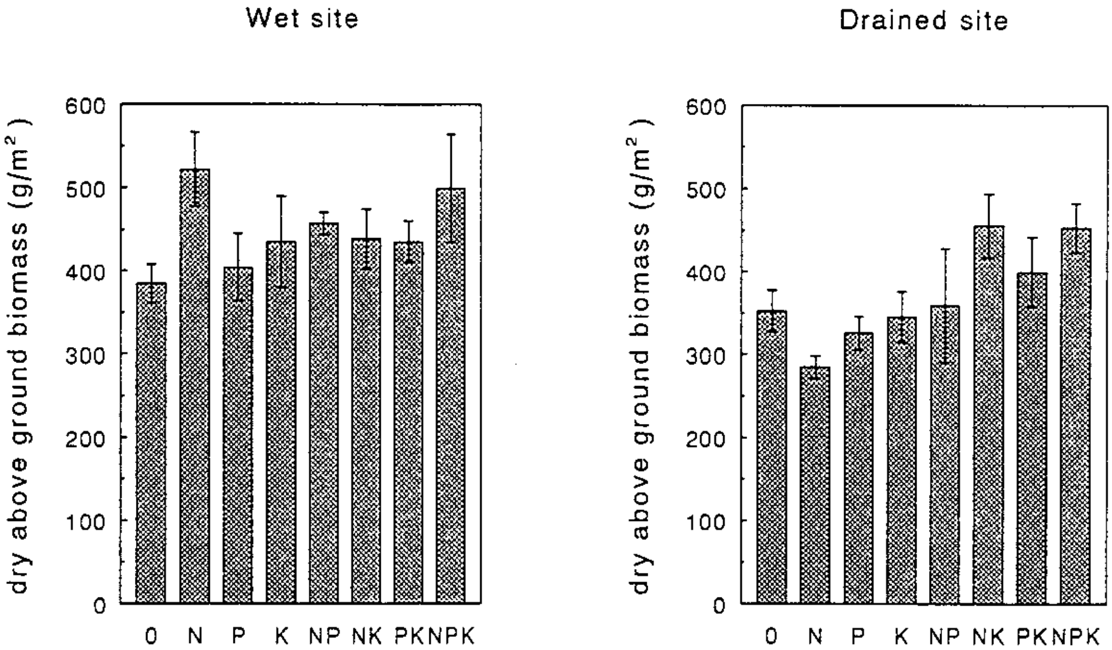

Figure 2. Above-ground biomass in both sites after full-factorial fertilization with N,P and K. Significance of differences was tested using a one-way ANOVA with Tukey contrasts ($n = 5$).

Table 3. Nutrient content of the above-ground dry plant material after different fertilization treatments in a wet, well-developed *Caricion curto-nigrae* and Significance of differences was tested using a one-way ANOVA with Tukey contrasts ($n = 5$).

Treatment	N-content (g kg^{-1})	P-content (g kg^{-1})	K-content (g kg^{-1})	N/P ratio	N/K ratio	K/P ratio
O	13.77±0.44 a	1.87±0.18 ab	9.65±0.86 ab	7.42±0.32 ab	1.47±0.12 bc	5.15±0.29 ab
N	14.17±0.56 a	2.04±0.13 ab	11.86±0.44 b	7.05±0.49 ab	1.20±0.04 ab	5.87±0.24 b
P	14.08±0.70 a	2.30±0.10 b	12.84±0.34 c	6.12±0.19 a	1.09±0.03 a	5.60±0.18 b
K	14.19±0.38 a	1.84±0.07 ab	10.23±0.30 a	7.79±0.43 b	1.39±0.05 abc	5.60±0.24 b
NP	15.05±0.49 a	2.31±0.24 b	13.12±1.08 c	6.66±0.45 ab	1.16±0.06 ab	5.74±0.30 b
NK	13.29±0.21 a	1.66±0.05 a	7.89±0.45 a	8.05±0.26 b	1.70±0.07 c	4.77±0.23 ab
PK	13.15±0.52 a	1.77±0.04 a	7.79±0.49 a	7.45±0.37 ab	1.70±0.08 c	4.40±0.24 a
NPK	14.86±0.77 a	2.13±0.13 ab	11.80±1.17 b	6.70±0.27 ab	1.29±0.08 ab	5.49±0.25 ab

Chemical analyses of plant material

Nitrogen fertilization in the wet site did not result in an increase in the N content (g/kg) of the plant tissue compared to the control (Table 3). The same was observed for fertilization with P or K, respectively.

In the drained site, additions of N and P also did not result in an increase in content of these nutrients (Table 4). But the effect of K fertilization was very obvious. Potassium addition increased the K content of the plant tissue ($p < 0.05$), but it decreased the P content ($p < 0.05$). The N:K ratio in the drained site increased ($p < 0.05$) compared to the control after N fertilization while it decreased ($p < 0.05$) after K-fertilization. This did not occur in the wet site.

Double pot experiment

The effect of omitting nutrients from a nutrient solution in different treatments is shown in Figure 3. Providing turf from the drained site with a complete nutrient solution caused a more than 5-fold increase in biomass

Table 4. Nutrient content of the above-ground dry plant material after different fertilization treatments in a drained, degraded site in the Zwarte Beek nature reserve. Significance of differences was tested using a one-way ANOVA with Tukey contrasts (n = 5).

Treatment	N-content (g kg^{-1})	P-content (g kg^{-1})	K-content (g kg^{-1})	N/P ratio	N/K ratio	K/P ratio
O	22.51±0.96 abc	3.59±0.16 cd	4.22±0.22 a	6.29±0.20 ab	5.37±0.26 b	1.18±0.06 a
N	25.29±0.59 c	3.34±0.10 abcd	3.29±0.27 a	7.59±0.17 d	7.88±0.65 c	0.99±0.07 a
P	23.69±0.89 bc	3.94±0.15 d	3.42±0.18 a	6.03±0.21 a	6.98±0.33 bc	0.87±0.02 a
K	18.70±0.47 a	2.86±0.09 a	9.66±1.03 b	6.57±0.24 abc	2.04±0.25 a	3.38±0.33 b
NP	25.58±1.42 c	3.48±0.14 bcd	4.04±0.36 a	7.34±0.18 cd	6.58±0.73 bc	1.17±0.13 a
NK	21.16±0.53 ab	2.78±0.10 a	11.07±0.91 b	7.62±0.13 d	1.96±0.15 a	3.96±0.25 b
PK	19.53±0.73 a	3.16±0.17 abc	9.36±0.61 b	6.20±0.11 ab	2.12±0.16 a	2.99±0.26 b
NPK	20.46±0.91 ab	2.95±0.13 ab	10.18±1.08 b	6.93±0.12 bcd	2.08±0.18 a	3.43±0.31 b

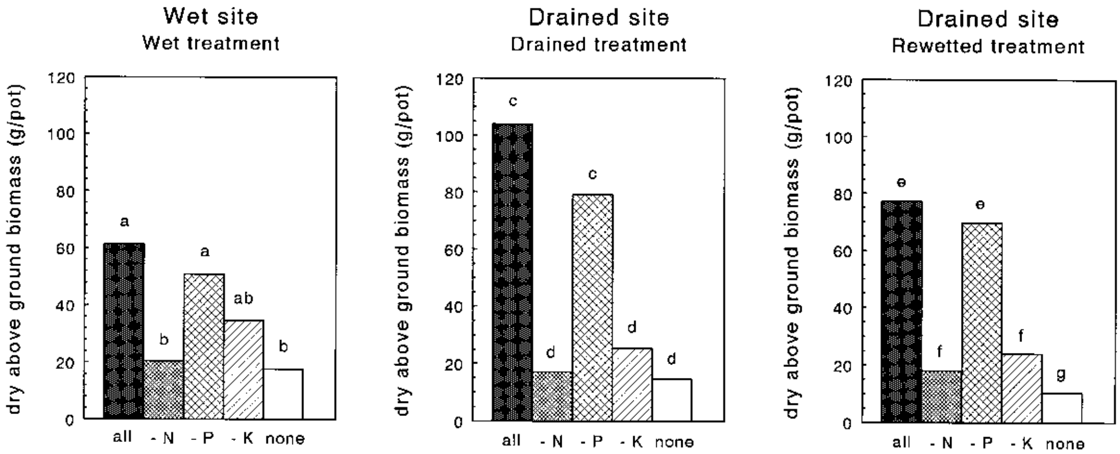

Figure 3. The effect of omitting nutrients (all = complete nutrient solution, -N = N-deficient, -P = P-deficient , -K = K-deficient, none = deficient for all three macro nutrients) from a nutrient solution on the above-ground dry biomass yield of intact turf samples in different treatments. Turf from a wet site with a well-developed *Calthion palustris* was treated wet; turf from a degraded, drained site was treated drained or rewetted. Bars with the same letter within one treatment were not significantly different ($p > 0.05$).

yield compared to the turf grown on water while the biomass increased only 3 times in the wet site.

In the wet treatment (turf taken in the wet site), omitting N from the nutrient solution resulted in a significant lower above ground biomass yield compared to the yield grown on complete nutrient supply while omitting P or K did not. In the drained and the rewetted treatment both N and K absence resulted in a dramatic decrease of the biomass. Omitting P from the solution did not result in a significant lower biomass in any of the treatments.

Rewetting the turf taken in the drained site only decreased the dry above-ground biomass production when grown on a complete nutrient solution. Rewetting when grown on other nutrient solutions or on H_2O did not result in a significant change in biomass.

The two-way ANOVA revealed that omitting nutrients had a strong effect on the above-ground biomass ($p < 0.001$). There was an interaction between nutrients and treatment when comparing the wet and the drained treatment ($0.01 < p < 0.05$). Comparison of the drained and the rewetted treatment showed only an effect of the different nutrient solutions ($p < 0.001$). No significant effects were found between the different treatments and no interactions were assessed between treatments and nutrient solutions.

Discussion

Effects of drainage on nutrient limitation

Our fertilization experiment under field conditions showed that plants in the drained site experienced K-limitation. Single K-fertilization did not cause a higher biomass yield than the control but combined with N and/or P it did while NP-fertilization resulted in a yield similar to the control. Also the K-content of the vegetation increased after K-fertilization. Plants in the undrained poor fen experienced N-limitation. The N-content of the vegetation did not change in the N-fertilized treatments in the wet site but N-supply stimulated the above-ground biomass. This means that all N, taken up by the vegetation, was used for growth. Boeye et al. (1997) found no important nutrient limitation in the same wet site based on fertilization treatments with N and P. Nevertheless, they also had indications for N-limitation based on nutrient ratios in the plant tissue. The experiment with intact turf confirmed the findings of our fertilization experiment in the field. Although the differences were much more pronounced than in the field experiment and samples of the drained site showed an additional N-limitation. This could be due to the experimental setup. A rooting zone of only 10 cm combined with repeated harvesting of the vegetation will result in a quicker depletion of the nutrient stocks.

Phosphorus seems sufficiently available for growth of the vegetation. This was evident from the fertilization experiment, the chemical analyses of plant material, and from the water quality measurements. Analyses of the groundwater in the study area indicated that the input of phosphate in the study area is relatively large. Measurement of redox potentials in the wet site indicate that iron will be present in reduced form most time of the year which means a higher solubility of iron phosphates.

Individual plant species reacted differently to fertilization. This was mainly observed in the wet site where the main increase after N application was due to *Filipendula ulmaria*. This was the only species reflecting the response of the vegetation. Other species reacted on P (*Potentilla palustris* and *Sparganium erectum*) or K (*Equisetum palustre* and *Potentilla palustris*). They probably coexist due to a difference in nutrient demand of the plant species or because each species uses specific ways to exploit the soil environment.

In our study area the vegetation in the drained site had a lower K content, which is the deficient nutrient, while the N and P contents were higher. Although the nutrient pool is lower than in the wet site, this may be caused by a higher mineralization rate in the drained site due to prevailing aerobic conditions.

Whether plant nutrient levels or nutrient ratios can serve as indicators for nutrient limitation remains debatable (Pegtel 1996) and if so, what are the threshold values. Koerselman & Verhoeven (1993), Wassen et al. (1995) and Koerselman & Meuleman (1996) state that nutrient ratios from plant tissues indicate limitation in fen vegetation. According to those authors, a ratio of less than 14 points to N-limitation and a ratio of more than 16 suggests P-limitation. In our wet site, N:P ratios then point to N-limitation, which is in accordance with our experiments. N:K ratios indicated that none of these nutrients or that both N and K are deficient. Pegtel (1996) calculated a limitation threshold value of 1.2 for the N:K ratio. The nutrient ratios of the vegetation from the drained site were much higher indicating clearly K-limitation. This also agrees with our experiments. The N:P ratio showed N rather than P-limitation. In our opinion, the latter observation is of limited value since K-limitation is seen as a main constraint.

Effects of rewetting

The results of the experimental rewetting showed no short-time changes in the type or extent of nutrient limitation. The rewetted turf samples from the drained site showed the same overall nutrient limitation (N and K) as the turf under drained conditions. Although the above-ground biomass in the rewetted series was lower in the drained series when grown on a complete nutrient solution, this is not regarded as a relevant difference. Apparently the plants from the drained site could not fully exploit the nutrients that were supplied. In the long term, succession is expected in the direction of a vegetation more adapted to wet, anaerobic conditions. The species composing this newly-developing vegetation might have different nutrient requirements resulting in another nutrient limitation in the future.

Restoration prospects

Our results confirm the results of Kayak & Okruszko (1990: *Lolio-Cynosuretum*), De Mars (1996: *Molinietum*), Pegtel (1996: a range of *Poo-Lolietum* to *Festuco-Cynosuretum*) and Van Duren (accepted: *Calthion palustris*) who found that severely drained peat soils are prone to K-limitation. Plant communities with different nutrient requirements and productivity endure similar problems after a long period of drainage, in which practically all characteristic species disappear. We found that rewetting does not lead to a rapid improvement of K-availability; the K-constraint for plant growth remains. This could mean that rewetting of severely drained peat soil will not automatically lead to a successful restoration. Kayak & Okruszko (1990) working on restoration of drained peat soils, indeed found that species-rich meadow vegetation types recovered only after K fertilization. However, for large-scale restoration projects K-fertilization is not an option. Removing the severely drained topsoil is also very expensive and has very dramatic consequences for the seed bank (Thompson et al. 1996). Renewed flooding with surface water may increase the K-pool but it will also increase P- and N-pools (Wassen et al. 1995a,b). The results will probably be an eutrophication. A combination of groundwater and surface water flooding is possibly the best solution for the restoration of severely drained peat soils.

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